MADROÑO

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Contents

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MIGRATION AND EVOLUTION IN PLANTS[1]

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It will be my objective to point out that the dynamics of the genetic elaboration of the plant population over the available habitats is the dynamics of natural selection and that genetic variation and natural selection together provide the dynamics of plant migration. Hence, plant migration and the organic evolution of each genetic lineage involved are concomitant.

The Concept of Migration

There are at least three different types of movement of natural populations, each of which may be spoken of as migration. There is the oscillating phenomenon such as the back and forth movement of ducks and geese wherein these animals migrate closely in tune with the seasonal progression of climate. This we may speak of simply as *seasonal migration*. Although these animals are adapted genetically to this mode of life, the dynamics of seasonal migration do not involve the simultaneous and obligate genetic elaboration of the population over area.

A second type of migration is the impulsive or sporadic movement of organisms possibly related to overpopulation phenomena. Here we have such phenomena as the curious suicidal migrations of the arctic lemming and the occasional mass migrations of excessively large populations of rodents such as the migration of mice in the San Joaquin Valley of California a few years ago. Such *sporadic migrations* do not necessarily involve the genetic elaboration of the population, although with the increase in density of the population there is probably a concomitant increase in its genetic variability.

A third type of migration is not seasonally oscillatory, but it may at times appear as though sporadic. It is often persistently directional through long time, and always involves the lineal succession of individuals. It may be either a response to secular environmental changes or to the local environmental selection of fortuitous adaptive changes that are products of genetic variation. More commonly, these changes operate together. Because such changes usually include occurrences on a scale of very long time periods even in terms of geological time, we may speak of this type of migration as *secular migration*.

Both seasonal and sporadic migration are known only in animals. Secular migration may occur in both animals and plants. For instance we have fossil evidence that both the camel and the horse originated in North America, where they are now extinct, and migrated to the old world, where they still persist in the form of changed modern descendants. We have

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[1] Presented as a semi-popular lecture in the "Symposium on Evolution" commemorating the Centennial of Mills College, Oakland, California, April, 1952.

similar evidence of the migration of plants which we are able to trace through the "flashes" of the fossil record and through which we may interpret the evolutionary changes that have taken place during this migration.

The important difference between secular migration and seasonal and sporadic migration is that secular migration, because it is involved with the linear reproductive succession of individuals through time, is obligately concerned with the genetic elaboration of the population over environments. Such genetic elaboration of the population over environments is a significant part of the migrational dynamics. This need not be the case with either seasonal or sporadic migration.

It is necessary that I make clear that migration and dispersal are not synonymous. Dispersal is the movement of an organism in any form from one place to another (Ridley, 1930). If, however, after dispersal, the individual is unable to survive and reproduce, there is no migration (Clements, 1916). At any given time with any species population the potential scope of dispersal is infinitely greater than is the potential scope of migration. Seeds regularly find their way into many habitats in which there is no chance of their survival. Perhaps the best examples are the hundreds of cultivated plants dispersed by man through cultivation which are unable to survive in the areas into which they are introduced except through the care given them by man. Assuming that activities associated with man's culture are artificial, such introduced plants are not regarded as part of the natural plant population. On the other hand, many of our weeds, dispersed through man's carelessness, became established and now are self-perpetuating populations. These are examples of effective steps in migration.

Dispersal beyond the habitat of the population provides that genetic variants, initiated in the population, may reach a new environment to which they may be adapted and by which they may be selected for survival. If the new area is contiguous to the old, the area of the population is extended, and the survival of the new variant may, through gene exchange, serve to stimulate the pattern of genetic variability of the population as a whole. If the new area is not contiguous a new, isolated or semi-isolated race is established.

It is also important that I point out that we have traditionally thought of secular migration in terms of the migration of floras and faunas (Chaney, 1936). Such apparent mass migrations are strictly coincidental insofar as dynamics are concerned. If we are to study and interpret migrations in terms of dynamics we must concern ourselves solely with the activities of successive individuals within interbreeding populations functioning under the influence of environmental conditions.

THE DYNAMICS OF MIGRATION

In a previous paper (Mason, 1946) I have pointed out that there are three aspects to the scope of the dynamics of any problem in plant geog-

raphy. First, there is the individual organism carrying on the vital proc-
esses that insure its survival and provide for the continuity of the popu-
lation. These vital processes are physiological in scope and they operate
in accordance with the theory of physiological limits and the principle of
limiting factors, and they are influenced by the conditions of the environ-
ment. Secondly, there is the genetics of the population which is concerned
with the actual gene exchange between individuals and the genic changes
that may result from any of the mutagenic agencies that may operate in
the populations. These may set the physiological capacity of the indi-
vidual with respect to its various functions. Thirdly, there is the environ-
ment as it varies over area and through time. The conditions of the envi-
ronment may function as barriers to migration or they may serve as
migration lanes. Through environmental control over physiological func-
tion the environment selects its plant population. This is, in effect, natural
selection.

THE PHYSIOLOGY OF THE INDIVIDUAL. The functioning of plants is
conditioned by the factors of the environment as they operate to control
physiological processes. The relationship between environment and pre-
cise physiological process is probably genetically fixed within each indi-
vidual plant as to the nature of the span of tolerance of the particular
environmental factors concerned. The fixation of the tolerance span may
result from any of the gene assorting and gene modifying mechanisms of
cytology and genetics as these operate to allocate a given set of genic
materials to each individual plant. Physiological characters, as imparted
by gene combinations, vary among the individuals of the population in
the same way that morphological characters do. They might and probably
do vary to the extent that many of the seeds produced are incapable of
functioning under the environmental regime in any of the available habi-
tats. However, they could function in some other habitat should chance
dispersal enable the seed to reach that habitat.

It is especially important to our thesis that we emphasize the role of
variation in physiological capacity of individuals of a population. The
vital physiological processes that go on within each individual plant oper-
ate within the basic structure of the theory of tolerance and the principle
of limiting environmental factors. It is because of this that there is a
close relationship between the plant and the environment. It is because of
the variation in physiological capacity and the role of limiting environ-
mental factors that different kinds of plants occur in different kinds of
habitats. We can speak broadly and say that some kinds of plants grow
only in the tropics while others grow only in the arctics. Or, as research
in this field advances, we can speak in increasingly precise terms. We now
know that species become elaborated over area in direct proportion to
their genetic diversity with respect to physiological characters on the one
hand and, on the other, to the degree that these variants become dispersed
into suitable habitats. The experimental work of Clausen, Keck and
Hiesey (1948) on *Achillea* gives ample evidence of this. Thus, individuals

comprising a species may be aggregated into populations that differ from one another to a greater or lesser degree. Today, facts discovered during the research of some of my students enable us to carry this even further. We may now state that the precise distributional pattern, even within some small interbreeding populations, reflects a pattern of genetic diversity in the physiological capacity of the individuals that have been selected by a pattern of local habitat variation. Some members of the same interbreeding population can survive through selection in one part of the area of the population, but would be rejected and perish in another part of the area of this same small population. It is because the physiological processes of plants operate within limits or extremes of environmental conditions that they are important in determining the area in which species can live. Since the range of tolerance is subject to the laws of evolution and genetics and is as characteristic of the plant as are its morphological characters, it is to be expected that there will be variation from one individual to another within the interbreeding population. Variation in tolerances thereby becomes the basis of explaining how the members of a species become elaborated over a complex set of environmental conditions, the total range of which is beyond the capacity of any one individual. Each individual is but an increment in the total range of the species. One individual may extend the tolerance of the species population in the direction of one environmental extreme while another individual will extend it in the direction of another extreme.

Thus the physiological processes of the plant, whether they involve nutrition, respiration, growth, or reproduction operate under the influence or sanction of the environmental conditions. The environmental condition circumscribes the area in which the function can operate. Variation in physiological capacity among individuals almost certainly demands that the plants will occupy different kinds of habitats.

THE GENETICS OF INDIVIDUALS IN POPULATIONS. The interbreeding population, through the physiological functioning of individuals and the mechanism of gene exchange, sets up a self-perpetuating dynamic system so that functioning individuals continually are being produced as old ones die. Because there are always individuals present, the population is said to persist. Persistence of the population and of the species is thus vested in the reproductive process of individuals of the population. For the most part, these processes are sexual processes which, because of their attendant cytological phenomena, set in motion the mechanics of population genetics. Persistence of the population is not guaranteed through population genetice, but no better device has as yet been produced to insure opportunity for survival in the face of fluctuating and changing environmental conditions. In meeting these situations, some populations have both migrated and undergone evolutionary changes. Other populations have not been genetically adaptable and have perished. I have previously pointed out (Mason, 1946) that genetics, by whatever mechanism it may operate, in each individual case functions to set the capacity of the plant to tolerate

the conditions of the environment. Once the zygote is formed, the potential individual will be capable of carrying on all of its vital functions only under the environmental conditions to which it may be thus preadapted. Usually seed grow only in an environment similar to that in which the parents grew, but genetic processes may result in production of seed having somewhat different capacities than those of the parents, capacities that enable the progeny to become established and survive in slightly different or new environments. Such new environments have nothing to do with the *preadaptation* of these seeds that become established there. They can only select or reject an already adapted individual. The role of genetics, so far as the potential characters of this individual are concerned, is ended with the formation of the zygote. Since reproductive processes continue in the population, we may think of the population as thereby being continuous beyond the life span of any single individual member. The continuity in reality is the many successions of individuals, overlapping in their duration.

That the relation between function and conditioning environmental factors is genetically fixed within each individual plant has been established through considerable research (Turesson, 1922; Clausen, Keck and Hiesey, 1940, 1948). However, no individual represents the total span of variation exhibited by the population as a whole. Breeding programs for earliness or lateness in agricultural crops in local situations are dealing essentially with the genetics of physiological characters. The fixing of the tolerance spans within individuals may result from any of the mechanisms operating in genetics which function to apportion gene materials among gametes.

Out of the mass of preadapted seed received, the environment permits the survival of only those which are capable of carrying on all of their vital functions under the conditions prevailing in that environment. This repeated selection, generation after generation, tends to fix the form and the physiological capacity of the mass of individuals that constitute the species population in that environment, and it tends to control the range of genetic variation within the species population. Thus any mutant in the population which has the potentiality of affecting physiological relations will soon be eliminated should it produce an effect that is not selected by the environment. On the other hand, should the mutant produce a better relationship with the environment, or should it enable the population to expand its area into new habitats, it will be favored and will tend to increase the genetic diversity of the population and thus increase the survival chances of the population in the face of environmental fluctuation and change. This is essentially the mechanism of natural selection.

Thus the genotypes within the species population become modified by environmental selection. This is what Turesson (1922) called, "genotypical response of the plant species to the habitat." Such selection results locally in a genetic race thoroughly in adjustment with its environment. It involves the pattern of interaction between the various factors of the

environment, the physiological processes of the plant concerned with germination and establishment and the various functions of individuals.

It is through these processes that the species is able to persist in a given environment through normal fluctuations of environmental conditions. Likewise it is through these genetic processes that variation develops, thus enabling the species to extend itself into new habitats. Only in this way can a migrating plant species overcome the diverse environmental conditions that it would encounter in its migration. Only in this way can we explain the habitat diversity between the species of a genus. In recognizing the role of genetics in plant migration, it is important to reemphasize the point that the seed destined to survive in a new environment arrived in that environment already adapted. Also it is important that we realize that the new environment played no part in this preadaptation. All of this happened through those genetic phenomena that are inherent in the reproductive process under the influence of the environmental relations of the parents.

THE NATURE OF ENVIRONMENT AND ENVIRONMENTAL RELATIONS. The medium in which the plant grows, involves chiefly the climate and the soils, but it may also include the direct and indirect effects of other organisms. The interaction of climate, soils, and organisms is very complex.

Climatic factors in any given region function within a general pattern of diurnal and seasonal rhythm, such as the daily fluctuations of temperature, or as temperature and rainfall follow a seasonal sequence, or as length of day and length of growing season follow a rhythmic sequence. Often these rhythmic sequences impose a rhythmic sequence on other environmental factors such as the position of the water table, or the salinity of lakes in seasonally arid regions. The nature of such sequential events may be limiting factors to some species of plants. Climatic factors usually occur over area as directional gradients of intensity or amount and no sharp boundaries exist. Where these appear to exist they are usually evidence of a local steepening of the gradient. The nature of these gradients in their effect upon plant populations often becomes selective locally to produce clines within the population with respect to the tolerance of these conditions. Each local race is adapted to the local area of the gradient. This is often evident in the gradient of length of season on the slopes of a mountain of sufficient height where a species occurs throughout. Those plants at low altitudes will be adapted to a long season while those at high altitudes will be adapted to a short season.

Edaphic factors are those pertaining to soil composition and condition. They operate within a situation imposed by local climate and to some extent they may be a product of that local climate. They may be relatively persistent features, expressible in terms of presence; they may vary locally in their intensity or amount; they may fluctuate as a result of chance climatic, biotic or diastrophic events; or they may follow a rhythmic pattern in tune with the rhythm of climate. The edaphic situation often has persistent features of large area such as may be determined by litho-

logic conditions, or by the position of the water table. Such features in turn produce effects upon soils to which they contribute. In conjunction with local climate, soils may be significantly altered and characterized by accumulations of salts at the surface. There are many ways in which edaphic situations may vary either within themselves or through their interactions with other environmental conditions. In any event, the areas occupied by given sets of edaphic conditions constitute the areas available to plants, and the mosaic of edaphic factors across area provides a significant set of variants for the operation of selection.

Biotic factors present many interpretational problems because the organism itself is subject to climatic and edaphic situations. Furthermore biotic effects may be either direct or indirect. When the influence of an organism is indirect, the organism creates a condition in another factor to which a second organism reacts. For instance a rodent may loosen the soil. The reaction of any plant that might be affected is to the loosened soil rather than to the rodent directly. Loosened soil due to other causes might produce the same effect in the plant.

It should be made clear that because they are often interrelated the problems of environmental factors and their conditioning effects are not simple. They are not solely matters of presence or absence of fluctuating intensities and demands, nor are they the simple problems of gradients between extremes. They may involve coincidences between two or more rhythmic cycles of fluctuating conditions, or fluctuating physiological demands, or of rhythmic sequences in the ontogeny of the plant. Often they serve to condition one another and in so doing, they may alter the physiological response.

When we consider all aspects of the environment, it becomes clear that much of its significance to our problem is the fact that environmental condition occupies area independently of whether or not the precise condition or combination of conditions may influence a particular organism. Thus area is subordinate to environmental condition in determining where a given species can grow. Of equal significance is the fact that environmental condition varies enormously over area, thus presenting a mosaic of conditions sometimes locally rather uniform, sometimes locally very complex. Each such local habitat is either the potential habitat of some chance genetic race of the species population, or it may present a barrier too great for a genetic race to cross by occupancy and successive seed dispersal.

It should be clear that environmental conditions as they occupy area present problems to any migrating species. The magnitude of some of these areas is such as to make it mandatory that the species cross by occupying the area. One individual seed may, by preadaptation and fortuitous dispersal, reach a suitable habitat in the area and become established. Before a second step can be taken normally, the reproductive process must take place to produce additional migrules. These, if they succeed, build a local interbreeding population.

In the process of migration, environmental diversity must be met and overcome through the development of individuals and races of the species population preadapted to the new environmental situations that are encountered in the migration. Although in general the population must cross such areas by inhabiting them, some fortuitous long-jump dispersal may at times occur. The greater the genetic diversity of the population, the greater are its chances of survival in the face of the hazards of migration. A genetically stable species has little chance of success as a migrant. We must bear in mind that migration is possible through successive genotypic changes which meet the pattern of the environment encountered. Climatic change usually makes it mandatory that the species population either migrate, become adapted to the change, or perish. Under conditions of climatic change, the species population may remain within range of the same climatic conditions by migrating in pace with the change. In so doing, however, it encounters very great edaphic diversity to which it must become accommodated or it will perish. Such a migrating population may leave behind descendant populations capable of adjustment to further climatic changes. These populations may become points of origin of further evolutionary diversification.

In conclusion, we may say that simultaneous with migration we usually find evolutionary diversification by means of genetic elaboration of the migrating lineages. Thus, the population is accommodated to the environmental diversity that it encounters. The interbreeding population provides the necessary reservoir of genic materials for recombination in varying manner. It thereby provides for the persistence of the species through adjustment to environmental fluctuation and change and for extending the area through genetic change. At length these changes may be of profound scope and be spoken of as evolution.

It is doubtful if any extensive long-term migration is possible without significant evolutionary change in physiological capacity. It seems probable that only plants undergoing active speciation are capable of extensive migration. It would seem therefore that an elaborate taxonomic and geographic pattern in any group of plants would stand as testimony of a former highly vigorous genetic nature.

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CHROMOSOME NUMBERS, APOMIXIS, AND INTERSPECIFIC HYBRIDIZATION IN THE GENUS TOWNSENDIA[1]

JOHN H. BEAMAN

The genus *Townsendia* Hooker, of the tribe Astereae of the Compositae, consists of about twenty species of small annual, biennial, or perennial, western North American plants. The genus was revised by Larsen (1927), but since that time several poorly understood taxonomic complexes have become apparent. Since no chromosome studies on any member of the genus had previously been reported, a cytotaxonomic study was initiated in an attempt to solve some of these problems through a better understanding of natural relationships within the genus.

As the study progressed, other problems, chiefly involving apomixis and polyploidy, were encountered. With the appearance of these complications came the realization that *Townsendia* is ideally suited for intensive studies directed toward a further understanding of the roles of hybridization, apomixis, and polyploidy in speciation. The genus has a relatively small number of species and a fairly limited range. Most species flower profusely and can be grown without difficulty in the greenhouse or garden. These advantages make it a convenient subject for experimental studies on some of the mechanics of evolution.

MATERIAL AND METHODS

The collections studied are listed by species in Table 1. Culture number, chromosome number, and source of collection are given. Voucher specimens are filed in the Herbarium of the State College of Washington.

The collections were grown in the greenhouse and most of them also in the experimental garden at Pullman, Washington. Seeds were germinated on moist filter paper in petri dishes, the young seedlings transferred to pots, and some of them later transplanted to the garden. Plants of some collections were transplanted from their natural habitat to the greenhouse

TABLE 1. CHROMOSOME NUMBER AND SOURCE OF *TOWNSENDIA* COLLECTIONS STUDIED.

Taxon	Culture	Chromosome Number, 2n	Source
T. anomala	33	18	WYOMING, Park Co.: near Holm Lodge on Crossed Sabre Ranch, 10 mi. east of the east entrance to Yellowstone National Park, *Beaman and Preece 503.*
T. arizonica	4	18	ARIZONA, Coconino Co.: 9 mi. east of Peach Springs, *Preece and Turner 2609.*
T. arizonica	5	18	ARIZONA, Coconino Co.: 2 mi. east of Ashfork, *Preece and Turner 2617.*
T. exscapa	46	18	ARIZONA, Coconino Co.: 1 mi. south of campgrounds at Park Headquarters, Grand Canyon National Park, *Jones 800.*
T. florifer	1	18	IDAHO, Custer Co.: Highway 93 near Custer-Lemhi Co. line, *Preece and Turner 2389.*
T. florifer	28	18	OREGON, Harney Co.: 3 mi. south of Wagontire, *Ownbey and Preece 3358.*
T. grandiflora	18	18	COLORADO, Larimer Co.: 2 mi. west of Bellvue, *Preece and Turner 2858.*
T. grandiflora	39	18	COLORADO, Boulder Co.: near summit of Flagstaff Mountain, *Beaman and Preece 509.*
T. incana	6	28	COLORADO, Gunnison Co.: 15.6 mi. west of Gunnison on Highway 50, *Preece and Turner 2795.*
T. incana	37	30	WYOMING, Fremont Co.: 16 mi. southeast of Dubois, *Beaman and Preece 507.*
T. leptotes	42	18	COLORADO, Grand Co.: 4.5 mi. west of Kremmling on U. S. Highway 40, *Beaman and Preece 513.*
T. mensana	38	18	WYOMING, Albany Co.: about 12 mi. southeast of Laramie on U. S. Highway 30, *Beaman and Preece 508.*
T. minima	3	27	UTAH, Kane Co.: 5 mi. west of Long Valley Junction on highways 14 and 89, *Preece and Turner 2462.*
T. montana	35	18	WYOMING, Teton Co.: on south side of Teton Pass, *Beaman and Preece 505.*
T. montana	29	36	OREGON, Wallowa Co.: near shore of Ice Lake, 5 mi. southwest of Wallowa Lake, *Beaman and Preece 500.*
T. Parryi	31	18	MONTANA, Park Co.: 8 mi. west of Livingston, *Beaman and Preece 501.*
T. Parryi	8	36	MONTANA, Park Co.: at Cooke Guard Station, near Cooke City, *Ownbey.*
T. Parryi	34	36	WYOMING, Park Co.: near Holm Lodge on Crossed Sabre Ranch, 10 mi. east of the east entrance to Yellowstone National Park, *Beaman and Preece 504.*
T. Rothrockii	44	36	COLORADO, Park Co.: on Hoosier Ridge, *Beaman, Weber, and Preece 516.*
T. spathulata	47	36?	MONTANA, Park Co.: Ram Pasture Mountain, on the Wyoming border, southeast of Cooke City, *Witt 1845.*

and garden. Polyethylene refrigerator bags were used for shipping living plants from the field to the laboratory.

Studies of microsporogenesis were made using buds collected in the field, the greenhouse, or the garden. Buds were fixed in Carnoy's fluid (6 parts absolute alcohol: 3 parts chloroform: 1 part glacial acetic acid) for one hour, then transferred to 70 per cent alcohol where they were stored at about 10°C. until time of examination. Some buds thus stored

have remained in satisfactory condition for eight months. From the 70 per cent alcohol, individual florets were transferred to a drop of aceto-carmine on a slide, macerated with a glass rod, and smeared by the application of considerable pressure to the coverslip.

Root-tip examinations were made from the primary root of germinating seedlings. The technique used for root-tip smear preparations was similar to that outlined by Speese and Baldwin (1952) for leaf smears. Root tips were first placed in water saturated with paradichlorobenzene for two hours, then washed in distilled water and fixed in Carnoy's fluid (3 parts absolute alcohol: 1 part chloroform: 1 part glacial acetic acid). They were stored in the fixative for from one day to two weeks. After fixation the root tips were hydrolyzed in acid alcohol (1 part concentrated hydrochloric acid: 1 part absolute alcohol) for fifteen minutes. After hydrolyzation they were returned to Carnoy's fluid for about fifteen minutes, then smeared in aceto-carmine by the method described above.

Some of the preparations of buds and root tips were made permanent by the method described by Sears (1941).

Iodine-crystal violet smear preparations of anthers and iodine-crystal violet sections of buds and root tips were tried, but satisfactory results were not obtained.

The camera lucida drawings of meiotic chromosomes were made at late prophase or metaphase. Those of mitotic chromosomes were made at metaphase, the only time when they are shortened sufficiently for counting. All drawings were made under an apochromatic oil-immersion lens of N. A. 1.30 and an initial magnification of 1800 times. The magnification of the figures is approximately 900 times.

Observations

Chromosome numbers of 2n = 18, 2n = 27, 2n = 28, 2n = 30, and 2n = 36 were found in the genus. This pattern of numbers indicates that the base number of chromosomes for the genus is nine. This fits well in the Astereae, where the base number nine is found also in the related genera *Aster* and *Erigeron*. The apparent exceptions in the regular progression of the polyploid series, found in *T. incana* where 2n=28 and 2n=30, will be considered under that species.

In the discussion of the species, first the diploid, then the polyploid taxa are considered. Species in which only root-tip examinations have been made are considered last.

Townsendia arizonica A. Gray. Two collections of this species were studied. Seeds were germinated in December, 1951; and in May, 1952, the plants started flowering. Plants in the greenhouse have flowered almost constantly from that time until the present. Several plants of Culture 5 developed large fasciations.

The plants of both collections were self-sterile. Nine bivalents were observed at metaphase I (fig. 2), and no irregularities were found in microsporogenesis.

TOWNSENDIA FLORIFER A. Gray. Two collections of this species were studied. The plants began flowering about four months after seed germination and continued for a period of from two to four months. After that time they died.

The plants were essentially self-sterile, although some viable seeds were produced by selfed plants. Nine bivalents were observd at metaphase I (fig. 3), and no irregularities were found in microsporogenesis.

TOWNSENDIA GRANDIFLORA Nutt. Two collections of this species were studied. Seeds of Culture 18 were germinated in March, 1952. This species requires a longer time to reach maturity than most other species, and only one plant has yet flowered.

Nine bivalents were observed at metaphase I (fig. 4), and no meiotic irregularities were found. It is not yet known whether the plants are self-fertile or self-sterile.

Plants of Culture 39 were transplanted from the field. None of these have yet flowered. Seeds collected in the field were germinated to supply root tips for examination. In this examination, 18 chromosomes were observed (fig. 11).

TOWNSENDIA LEPTOTES (A. Gray) Osterhout. One collection of this species was studied.. The plants were transplanted from the field. In the greenhouse the plants initiated buds, but these did not reach the meiotic stage. Buds for examination were obtained from plants grown in the garden.

Nine bivalents were observed at metaphase I (fig. 5), and no meiotic irregularities were found. It is not yet known whether the plants are self-fertile or self-sterile.

TOWNSENDIA ANOMALA Heiser. One collection of this species was studied. It is from the type locality, the only station from which *T. anomala* is known. Young plants were transplanted from the field. Plants in the greenhouse became much more elongate than those in their natural habitat. This elongation probably resulted from insufficient light, since most growth in the greenhouse took place during the winter. A higher-than-normal water supply in the greenhouse also may have been partially responsible.

These plants were self-sterile. The study of microporogenesis was made from buds collected in the field. Nine bivalents were observed at metaphase I (fig. 1). In a few of the cells examined, chromatin bridges were seen after anaphase II. This irregularity probably indicates inversion of a chromosome segment.

TOWNSENDIA MENSANA M. E. Jones. This species was treated by Larsen (1927) as *T. sericea* Hook., but that name, as originally defined by Hooker, included the type of the earlier *Aster exscapus* Rich. [=*T. exscapa* (Rich.) Porter], and is therefore invalid (Cronquist, unpublished) under Article 65 of the International Code of Botanical Nomenclature.

Several collections of this species were grown in the greenhouse, but,
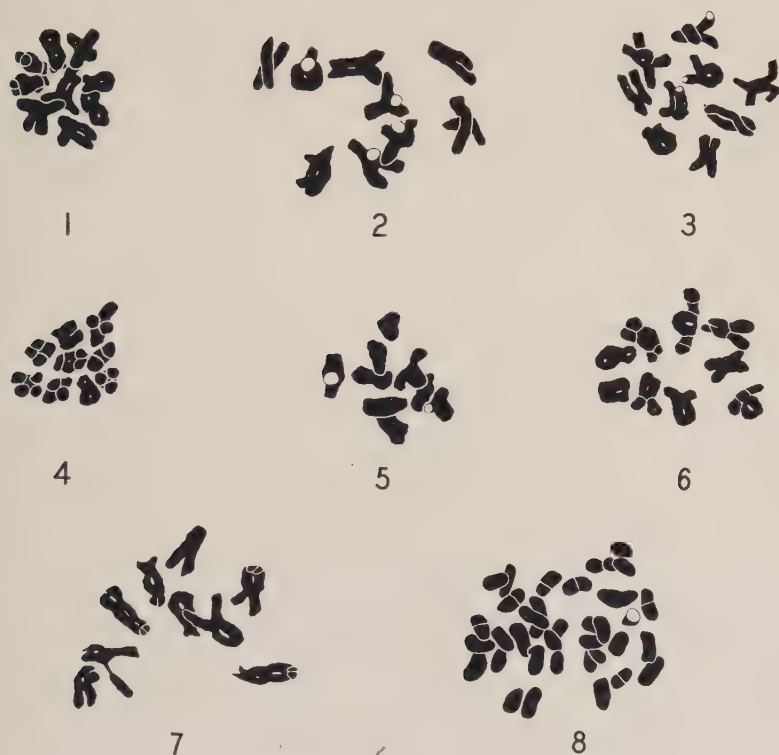
FIGS. 1–8. Meiotic chromosomes of *Townsendia*. FIG. 1. *T. anomala* (Culture 33). FIG. 2. *T. arizonica* (Culture 4). FIG. 3. *T. florifer* (Culture 28). FIG. 4. *T. grandiflora* (Culture 18). FIG. 5. *T. leptotes* (Culture 42). FIG. 6. *T. mensana* (Culture 38). FIG. 7. *T. montana* (Culture 35). FIG. 8. *T. montana* (Culture 29). All × 900.

like *T. leptotes*, the plants initiated buds which did not mature. One bud was obtained from a plant which was cold-treated by being placed out-of-doors for about three months during the winter. This bud was collected while the plant was being cold treated.

Numerous meiotic irregularities were found in the material examined; univalents were present in a large number of cells, micro-nuclei occurred frequently, and chromatin bridges after anaphase I were common. The weather conditions to which the material was exposed may have led to the meiotic irregularities, and an examination of additional material will be necessary before any conclusions can be drawn concerning the frequency of irregularities in this species.

Some cells were found in which there were no apparent irregularities, and nine bivalents were observed at metaphase I (fig. 6).

It is not yet known whether the collections at hand are self-sterile or self-fertile.

TOWNSENDIA MONTANA M. E. Jones. Two collections of this species

were studied. The plants of Culture 35 (from Teton Mountains) were self-sterile. Nine bivalents were observed at metaphase I (fig. 7), and no irregularities were found in microsporogenesis. Root-tip material of this collection also was examined and 18 chromosomes were observed (fig. 15).

An examination of microsporogenesis in plants of Culture 29 (from Wallowa Mountains) showed that they are tetraploid with $2n = 36$ (fig. 8). Although the chromosomes were frequently clumped, they were never found associated as bivalents. In prophase, as early as chromosomes were distinctly visible, only univalents were seen.

Generally there was only one meiotic division in this material. After this division cytokinesis took place, and a diad of microspores resulted. The two microspores split apart shortly after cytokinesis. Occasionally three nuclei resulted from meiosis, and when this happened one of the nuclei was often smaller than the other two. Tetrads of microspores also were formed, but they were uncommon.

Evidence which indicates that these plants are apomictic was obtained. This evidence is presented in a later section.

On several minor morphological characters plants of Culture 29 differ from those of Culture 35. Further studies may show that the two collections represent separate varieties or species on both cytogenetic and morphological grounds.

TOWNSENDIA PARRYI Eaton. Three collections of this species were studied. Both diploid and tetraploid forms are represented in the collections.

Culture 31 was collected when the plants were not in flower and only two plants were obtained. These plants were self-sterile. Nine bivalents were observed at metaphase I (fig. 9), and no irregularities were found in microsporogenesis.

Cultures 8 and 34 are tetraploid with $2n = 36$ (fig. 10). As in tetraploid *T. montana*, the chromosomes were not paired at meiosis. Chromosome clumps also occurred frequently. In contrast to tetraploid *T. montana*, in which the microspores were formed in diads, tetrads of microspores regularly were formed in *T. Parryi*.

Cultures 8 and 34, like the collections of *T. grandiflora*, required a longer period to reach maturity than most other species. The first heads were produced on some plants about eight months after seed germination. Other plants of these collections required an even longer period for development. The plants flowered for a period of from two to four months, then died.

Evidence that the two tetraploid collections of this species are apomictic was obtained and is presented in a later section.

TOWNSENDIA INCANA Nutt. Two collections of this species were studied. Plants of Culture 6 produced their first heads about four months after germination. Greenhouse plants which started flowering in March, 1952, have flowered continuously up to the present. Meiosis in this culture was found so irregular that no pollen-mother-cell chromosome count

was made. As many as nine bivalents were seen in some cells, but in addition there were univalents and chromosome clumps which could not be analyzed.

In an examination of root tips, the chromosome count 2n=28 (fig. 12) was obtained. This number is at variance with what would be expected in a polyploid series with a base number of nine, and it is likely that the collection represents a group of plants which are triploid with one extra chromosome. Evidence to support this hypothesis is outlined as follows:

1. The taxon is very similar morphologically to other taxa in the genus which have a base number of nine. It is especially close to *T. arizonica*.
2. Another triploid collection has been found in the genus.
3. Both bivalents (nine were seen in one cell) and univalents are found in the same pollen mother cell.
4. Evidence that the plants are apomictic was obtained.
5. In apomicts the abnormal chromosome complement would offer no difficulties in reproduction.

If the plants are of triploid constitution, it is also likely that they are alloploids. Evidence for alloploidy is found in the mitotic karyotype (fig. 12) where two chromosomes are conspicuously shorter than the others. These two chromosomes probably represent an homologous pair from two similar genomes. The absence of a third short chromosome suggests that the third genome is different from the other two and has been introduced through hybridization.

Culture 37 of *T. incana* was transplanted from the field. A study of microsporogenesis was made from buds collected both in the field and in the greenhouse. However, no accurate chromosome count was obtained because of chromosome clumping. As in the tetraploid *T. montana* and *T. Parryi* collections, there was no indication of chromosome pairing. Although asynapsis appeared complete, chromatin bridges were observed after both anaphases I and II. Formation of bridges suggests that at least partial synapsis must occur. Further study is necessary for a more complete understanding.

In an examination of root tips, the chromosome count 2n = 30 (fig. 13) was obtained. This number, like 2n = 28, does not fit in a polyploid series based on nine. It is likely that the plants are triploid plus three extra chromosomes.

In contrast to Culture 6, plants of Culture 37 cannot readily be considered alloploids. In the karyotype of this collection (fig. 13), three very short chromosomes are apparent. These short chromosomes could indicate three similar genomes (autoploidy), or one of them could be a duplicated chromosome. If the latter is the case, alloploidy is still possible.

An interesting feature about plants of Culture 37 is that they produced no pollen. A fairly large number of microspores were found in the anthers shortly after the tetrads had broken apart. At later stages fewer and fewer microspores or pollen grains were found. By the time of anthesis, no pollen was observed, and the anthers had started drying up.
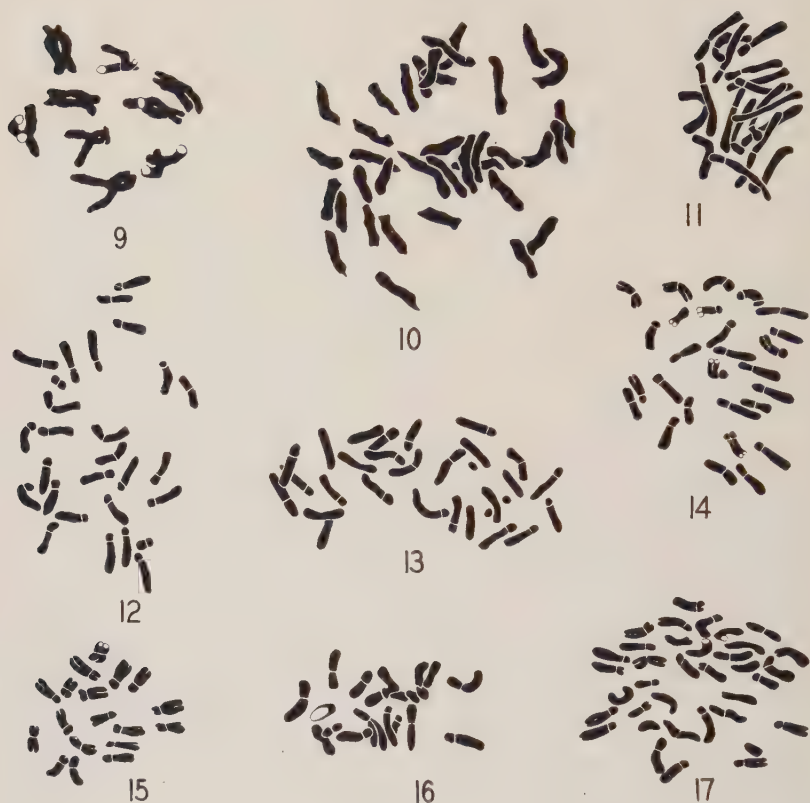
Figs. 9–10. Meiotic chromosomes of *Townsendia*. Fig. 9. *T. Parryi* (Culture 31). Fig. 10. *T. Parryi* (Culture 8). All × 900.

Figs. 11–17. Mitotic chromosomes of *Townsendia*. Fig. 11. *T. grandiflora* (Culture 39). Fig. 12. *T. incana* (Culture 6). Fig. 13. *T. incana* (Culture 37). Fig. 14. *T. minima* (Culture 3). Fig. 15. *T. montana* (Culture 35). Fig. 16. *T. exscapa* (Culture 46). Fig. 17. *T. Rothrockii* (Culture 44). All × 900.

Evidence indicating that the plants of the two collections of *T. incana* are apomictic is presented in a later section.

Townsendia minima Eastwood. One collection of this species was studied. These plants, like those of *T. leptotes* and *T. mensana*, initiated buds which did not mature. A three-months cold treatment during the winter was used to induce flowering.

In an examination of microsporogenesis, meiosis was found so irregular that no chromosome count could be made. Most of the chromosomes were badly clumped, but in some pollen mother cells bivalents and univalents were seen. In an examination of root tips it was found that the plants are triploid with $2n = 27$ (fig. 14).

Evidence indicating that the plants of this collection are apomictic is presented in a later section.

OTHER SPECIES STUDIED. In the following species, no buds were available for studies of microsporogenesis, and chromosome counts were made from root-tip preparations. These species with their culture number and chromosome number are: *Townsendia exscapa* (Rich.) Porter, Culture 46, 2n = 18 (fig. 16); *Townsendia Rothrockii* A. Gray, Culture 44, 2n = 36 (fig. 17); and *Townsendia spathulata* Nutt., Culture 47, 2n = 36 (?). A further study of these species is planned when buds become available.

APOMIXIS

Heiser (1948) first suggested the possibility of apomixis in *Townsendia*. In examining herbarium specimens of *T. scapigera*, he noted two very different population complexes in California. He found that specimens from Inyo County were dwarf plants, while those from the Sweetwater Mountains were large. In this connection, he stated: "Examination of the pollen of the latter [Sweetwater Mountains] specimens revealed a high percentage of empty grains, as well as the presence of both 3- and 4-pored grains similar to those found in many apomictic species."

During the course of the present study, apomixis was first suspected to be one of the mechanisms of reproduction in *Townsendia* when study of microsporogenesis in tetraploid *T. Parryi* (Culture 8) showed the chromosomes to be completely asynaptic; that is, only univalents were found at meiosis. Plants of this culture were found to produce large quantities of viable seeds even after cross-pollination was prevented. Because of the asynaptic condition it was concluded that these seeds were produced apomictically rather than as a result of fertilization. Diploid plants with regular pairing produced few or no seeds when cross-pollination was prevented. Thus in *Townsendia,* production of many viable seeds by non-cross-pollinated plants may be considered to suggest apomixis in those plants.

Since the first observation of asynapsis in *T. Parryi,* partial or complete asynapsis has been found in plants of six other collections. These collections are: *T. incana,* Culture 6; *T. incana,* Culture 37; *T. mensana,* Culture 38; *T. minima,* Culture 3; *T. montana,* Culture 29; and *T. Parryi,* Culture 34. With the exception of *T. mensana* (which has not been tested) non-cross-pollinated plants of these collections produced viable seeds. It also was found that these plants produce a uniform progeny. The presence of asynapsis, the production of viable seeds without cross-pollination, and the production of a uniform progeny strongly suggest apomixis in these collections.

Further evidence for apomixis in two collections (*T. Parryi,* Culture 8 and *T. incana,* Culture 6) was obtained by means of a rather simple experiment. Heads were treated by removing the corolla, stamens, and style from each disk floret. The ray florets likewise had the corollas and styles removed. This treatment was made before pollen in any of the florets had turned yellow. Development of the achenes was apparently normal in spite of the treatment, and there was a high percentage of viability of the seeds.

In order to correlate pollen quality with apomixis and sexuality in the genus, a study of the pollen of several apomicts and several sexual species was made. In Table 2 the quality of pollen from one plant of each of these cultures is shown. The pollen quality in the apomicts is very low in comparison to that of the sexual species and provides additional evidence that seed formation in some species of the genus must be possible without fertilization.

Five lines of evidence indicating apomixis in *Townsendia* may be summarized as follows:

1. Asynapsis.
2. Production of many viable seeds by non-cross-pollinated plants.
3. Production of a uniform progeny.
4. Seed development in spite of removal of stamens and styles from florets.
5. Low pollen quality.

During the study of pollen quality, it was observed that the pollen-grain size for each species was relatively constant. Diameter measurements of fresh pollen grains were therefore made. Twenty-five good (as defined in Table 2) pollen grains from one plant of each species were

TABLE 2. COMPARISON OF POLLEN QUALITY AND SIZE OF SOME APOMICTS AND SEXUAL SPECIES.

Taxon	Culture	No. of grains counted	No. of good* grains	Per cent of good* grains	Mean diam. of good* grains in microns	Standard deviation
Apomictic						
T. incana	6	358	45	12.6	48.1	± 1.8
T. incana	37	no pollen produced†	......	......	......	....
T. minima	3	379	69	18.2	38.9	± 0.8
T. montana	29	329	4	1.2	43.1	± 5.6
T. Parryi	8	352	225	63.9	46.0	± 2.7
Sexual						
T. anomala	33	466	458	98.3	23.6	± 1.5
T. arizonica	5	376	368	97.9	28.9	± 1.3
T. florifer	1	372	359	96.5	26.7	± 1.5
T. leptotes	42	393	377	95.9	26.5	± 0.9
T. mensana	38	484	412	85.1	23.5	± 1.2
T. montana	35	348	332	95.4	25.8	± 1.1
T. Parryi	31	387	384	99.2	26.3	± 1.5

* If a nucleus, or nuclei, could be seen in a grain after it was stained for one hour in aceto-carmine, it was considered good.

† See under discussion of *T. incana,* Culture 37.

measured. The spicules were not included in the measurements. An ocular micrometer and 900 times magnification were used for measuring. The mean diameter and standard deviation in microns of the pollen grains of each species studied are given in Table 2.

The tabulations of pollen quality and size show some very striking differences between the apomicts and the sexual species. The knowledge of these differences should be useful in subsequent studies when it may be

TABLE 3. COMPARISON OF POLLEN QUALITY OF HYBRIDS WITH THAT OF THE PARENTS

Taxon	No. of grains counted	No. of good* grains	Per cent of good* grains
T. arizonica × *T. florifer*	685	360	52.6
T. florifer × *T. arizonica*	664	223	33.6
T. arizonica	376	368	97.9
T. florifer	372	359	96.5

* If a nucleus, or nuclei, could be seen in a grain after it was stained for one hour in aceto-carmine, it was considered good.

necessary to distinguish between apomictic and sexual plants on the basis of pollen from herbarium specimens.

A study of the embryology of *Townsendia* should be very helpful in understanding apomixis in the genus. No work along this line has been attempted, but embryological studies are planned as a future project.

INTERSPECIFIC HYBRIDIZATION

Cross pollinations have been made among several diploid, self-sterile species, but this work is only in its preliminary stages. Extensive crossing, involving sexual species and the apomicts as well, is planned as a future project. Hybridization experiments should yield information concerning apomixis, natural relationships, and evolution within the genus.

Small quantities of apparently viable seeds were obtained from the crosses listed below and their reciprocals:

T. anomala (Culture 33) × *T. arizonica* (Culture 5)
T. anomala (Culture 33) × *T. montana* (Culture 35)
T. arizonica (Culture 5) × *T. florifer* (Culture 1)
T. arizonica (Culture 5) × *T. montana* (Culture 35)
T. arizonica (Culture 5) × *T. Parryi* (Culture 31)
T. florifer (Culture 1) × *T. montana* (Culture 35)
T. florifer (Culture 1) × *T. Parryi* (Culture 31)
T. montana (Culture 35) × *T. Parryi* (Culture 31).

One hybrid plant, *T. arizonica* × *T. florifer,* and one plant of the reciprocal were grown to maturity. The two plants were similar morphologically and intermediate between the parents.

Study of meiosis in the hybrids revealed no irregularities. Chromosome pairing was apparently as regular in them as in the parents. In contrast to this lack of difference at meiosis, an examination of pollen of the hybrids and the parents revealed a very significant difference in their pollen qualities. This difference is shown in Table 3.

SUMMARY

Cytogenetic studies were made in thirteen species of *Townsendia,* represented by twenty collections. Chromosome counts were obtained from studies of microsporogenesis and from examination of root tips. The chromosome numbers $2n = 18$, $2n = 27$, $2n = 28$, $2n = 30$, and $2n = 36$ were found in the genus. It is concluded that the base number is nine.

In the diploid collections, which are self-sterile, meiosis is usually regular, with nine bivalents at metaphase I, and pollen quality is high. In four polyploids, meiosis is irregular with univalent formation up to complete asynapsis, chromatin bridges, and the occurrence of only one meiotic division in microsporogenesis. These polyploids were found to be apomictic. Characteristically they form unreduced pollen through failure of synapsis and may be detected by their poor pollen quality and ability to set seed without cross pollination. Removal of stamens and styles from florets at an early stage did not prevent production of viable seeds. The pollen grains of the polyploids are distinctly larger than those of the diploids.

Hybrid seeds were obtained from cross pollination of several diploid, self-sterile species. One hybrid plant, *T. arizonica* × *T. florifer*, and one plant of the reciprocal were grown to maturity. Chromosome pairing was found as regular in the hybrids as in the parents, but hybrid pollen quality was low.

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BRYOPHYTA OF SANTA CATALINA ISLAND, CALIFORNIA

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Like most insular floras, that of Santa Catalina Island has attracted a large amount of botanical attention which, of course, has been stimulated by the high degree of endemism there. The comprehensive survey of the flora by Millspaugh and Nuttall (1923) covers all groups of plants, including the Bryophyta, and reviews the older literature. A more recent paper by Sayre (1940) lists the mosses collected by T. D. A. Cockerell (1938) on Santa Catalina Island, as well as on other islands off the coast of California. Some of the records cited by Millspaugh and Nuttall, as well as new collections, are included in the standard manuals of American mosses and hepatics (Grout, 1928–1940; Frye and Clark, 1937–1948) and by Koch (1950) in his check-list of the mosses of the state of California. In these several works we find eight species of Hepaticae and approximately thirty species of Musci reported definitely from Santa Catalina Island.

During the annual field meeting held jointly by the California Botani-

cal Society and the Southern California Botanists, the present author had the opportunity to visit Santa Catalina Island, May 1–3, 1953, and to collect bryophytes intensively in the vicinity of White's Landing, some five miles north of Avalon. Excellent habitats for mosses and hepatics occur on the rocky headland at the Landing, in the open, pastured valley behind it, and especially in the deep, precipitous, shaded canyons opening into the valley. About sixty species of bryophytes were brought back from this relatively small area, thereby nearly doubling the previously known bryophytic flora of the island. Of the eight species of Hepaticae reported by Millspaugh and Nuttall (1923), five were recollected, and five more can now be added as new to the island. Ten of the some thirty species of Musci reported from the island by various authors were not found again in the limited area studied, but twenty-eight other species not previously known were discovered. Since our knowledge of the bryophytes of Santa Catalina Island has been extended rather considerably through the activities of the California Botanical Society, it would seem appropriate to submit here a brief review of the previous reports and a list of the 1953 collections.

The discovery of nearly sixty species of bryophytes in a relatively small part of a large island in so short a time indicates that a careful survey of the whole island during a more favorable season would be very rewarding, and that the bryophyte flora must be much richer than realized formerly. Furthermore, there is a strong possibility that endemic species will be found. The first week in May was obviously too late in the season for the collection of bryophytes, in their best condition either in terms of morphology or of visibility. Because of the long drought, the plants in exposed habitats were completely dried out, very inconspicuous, and many of them had died. February, March, and even April would undoubtedly be better months for field studies of bryophytes, since at that season the sporophytes would be mature, yet many ephemeral species that disappear later might still be in evidence. Nevertheless, the 1953 collections not only increased substantially the known bryophyte flora of Santa Catalina Island but also resulted in the first records for California of two species, one of which is a Mexican *Riccia* previously unknown in the United States. Several of the species are so rare that the present material represents the first or second rediscovery since the original collection upon which the species was based. In their geographical distribution in California, the species fall into several categories. The largest floristic group consists of widely distributed, sometimes almost weedy species of drier habitats. More interesting elements are the species of very restricted distribution in the mountains of southern California, and those otherwise known only as far south as Marin or Monterey counties that now appear to have a very disjunct distribution in the state. Extensive collection of bryophytes on Santa Catalina Island is almost certain to result in the discovery of endemic species, and of a close correlation between the types of distribution of bryophytes and of flowering plants.

The following list contains all Bryophyta known definitely to occur on Santa Catalina Island. With few exceptions the names follow the most recent manuals (Grout, 1928–1940; Frye and Clark, 1937–1940). Species new to the flora of the island are indicated with an asterisk (*). The specimens upon which this report is based are deposited in the Dudley Herbarium of Stanford University.

HEPATICAE

PORELLACEAE

*PORELLA BOLANDERI (Aust.) Pears. On shaded rock-face above stream in deep canyon. This collection appears to represent the southernmost locality known for the species.

FRULLANIACEAE

FRULLANIA CATALINAE Evans. Not uncommon on shaded rock-faces and on the trunks of trees in canyons, at higher altitudes; with abundant perianths. This species, described by Evans (1897) from material collected Sept. 8, 1893, "on rocks in a cañon," does not seem to have been found subsequently until recollected in 1953. Recently, it has been reduced to the status of a synonym of *F. inflata* Gottsche (Clark and Svihla, 1944; Frye and Clark, 1947). On the basis of the present observations, however, *F. catalinae* appears to be adequately distinctive, even in the field, especially because of its conspicuously squarrose leaves, one of the characteristics emphasized by Evans.

FOSSOMBRONIACEAE

*FOSSOMBRONIA HISPIDISSIMA Steph. On shaded soil, rocky headland near shore; with sporophytes. The gametophytes of this hepatic die after the onset of the dry season and become conspicuously white. The setae in these specimens had not elongated at all and the capsules remained wrapped in the pseudoperianth and the apical leaves of the plant; the spores could escape only through the wearing away of the dead leaves and the dehiscence of the capsule wall. Perhaps in unusually rainy or foggy years the seta elongates in a normal fashion. However, it is interesting that this usually mesophytic hepatic can adjust itself successfully to reproduction under xeric conditions.

FOSSOMBRONIA LONGISETA Aust. This species, not recollected in 1953, was reported by Millspaugh and Nuttall, but their report may really represent the preceding species, already the source of some confusion (Evans, 1923).

REBOULIACEAE

ASTERELLA CALIFORNICA (Hampe) Underw. This species is relatively abundant on shaded soil and rocks in many places investigated; with archegoniophores and spores. Reported by Millspaugh and Nuttall.

ASTERELLA PALMERI (Aust.) Underw. Reported from Cottonwood

Canyon by Millspaugh and Nuttall, but not found in the vicinity of White's Landing in 1953.

TARGIONIACEAE

TARGIONIA HYPOPHYLLA L. Found in all parts of the area studied, usually on steep shaded banks; with involucres. A common hepatic, widely distributed through the drier and warmer parts of the world; reported by Millspaugh and Nuttall.

RICCIACEAE

RICCIA CRYSTALLINA L. (*R. catalinae* Underw.). Reported by Millspaugh and Nuttall on the basis of *R. catalinae*, whose original description gives no details of locality; not found in 1953.

*RICCIA NIGRELLA DC. The most common and abundant species on exposed soil on the headland at White's Landing; easily recognized in the field by the glossy, purple-black scales that become especially conspicuous as the plants dry out; identification confirmed by Dr. Ronald L. McGregor.

*RICCIA SOROCARPA Bisch. In very small quantity on exposed soil, rocky headland at White's Landing; identified by Dr. Ronald L. McGregor.

RICCIA TRICHOCARPA Howe. Kingman's collection of this hepatic at Avalon was reported by himself (1911) and by Millspaugh and Nuttall. Abundant on the rocky headland at White's Landing, it becomes conspicuous from the long white hairs that clothe the margins of the plants as well as the upper surface of the thallus over the sunken sporophytes.

*RICCIA VIOLACEA Howe. Found only in small quantity on the rocky headland at White's Landing, on exposed soil. This essentially tropical species (cf. Howe, 1923), not reported earlier from the United States, is not included in "The Hepaticae of North America" (Frye and Clark, 1937–1948). It was recognized, however, because of some collections made the preceding year in Baja California, Mexico: on the mainland in a deep arroyo several miles south of Puerto de Bahía de los Muertos (*Steere 17562*, April 2, 1952) and on Ceralbo Island, in the Gulf of California, in a large arroyo on the west side (*Steere 17563, 17567*, April 4, 1952). Dr. Ronald L. McGregor very kindly identified the Mexican collections and confirmed the present one.

ANTHOCEROTACEAE

ANTHOCEROS PEARSONI Howe. Reported without locality data by Kingman (1911) and by Millspaugh and Nuttall. Small fragments of some species of *Anthoceros*, collected on the steep bank of a deep canyon in 1953, were inadequate for identification.

MUSCI

FISSIDENTACEAE

FISSIDENS LIMBATUS Sull. Very common and abundant in moist shaded

habitats from sea level upwards; with sporophytes. Previously reported by Millspaugh and Nuttall.

DITRICHACEAE

CERATODON PURPUREUS (Hedw.) Brid. On soil over rock, steep bank; with sporophytes. A cosmopolitan weed whose absence from the island would be more noticeable than its presence; reported by Sayre.

DICRANACEAE

ANISOTHECIUM VARIUM (Hedw.) Mitt. Not uncommon on moist silt banks near small stream in deep canyon; with sporophytes. Reported (as *Dicranella varia*) by Millspaugh and Nuttall.

ENCALYPTACEAE

*ENCALYPTA VULGARIS Hedw. var. MUTICA Brid. This moss, common and widely distributed elsewhere in California, was collected in small quantity and in sterile condition on moist silt near the stream in a deep canyon.

POTTIACEAE

ALOINA AMBIGUA (BSG). Limpr. Abundant on rather exposed silt banks in deep canyon; with sporophytes. Previously reported from the same area by Millspaugh and Nuttall.

*ALOINA RIGIDA (Hedw.) Kindb. var. PILIFERA (BSG.) Limpr. On exposed soil, summit of rocky headland at White's Landing; rather abundant and with sporophytes.

*ANOECTANGIUM OBTUSIFOLIUM (Broth. & Paris) Grout. On vertical silt bank near small stream, upper reaches of canyon at perhaps 1000 feet altitude; sterile. This species is new not only to Santa Catalina Island but also to California. Its previously known geographical range comprises Texas, Arizona, and Mexico.

*BARBULA BRACHYPHYLLA Sull. On soil, steep bank in deep canyon; with sporophytes. This is a Californian species of restricted distribution.

*BARBULA CONVOLUTA Hedw. On moist soil near water, in deep shaded canyon; one small collection without sporophytes.

BARBULA CYLINDRICA (Tayl.) Tayl. On moist soil, steep bank in canyon; not rare but less abundant than the following species; with sporophytes. Reported (as *B. subfallax*) by Millspaugh and Nuttall.

BARBULA VINEALIS Brid. A common and almost weedy species in all the places visited (and in most of California); with sporophytes in several stages of development. Reported by Millspaugh and Nuttall from a Kingman collection, without locality. Probably most of the collections of *B. artocarpa* reported by the same authors belong here (Steere, 1939), although some of the collections may possibly represent *B. brachyphylla*.

DESMATODON CONVOLUTUS (Brid.) Grout. Abundant on soil, rocky headland at White's Landing; with sporophytes. Reported by Millspaugh and Nuttall (as *Tortula atrovirens*).

DESMATODON GUEPINI BSG. Reported by Millspaugh and Nuttall, but not found in 1953.

DESMATODON HENDERSONI (Ren. & Card.) Williams. Abundant on moist to wet soil on vertical banks near small stream, in deep canyon; only rarely with a few sporophytes. The complete description and excellent illustration of this species by Williams in the comprehensive work of Millspaugh and Nuttall, escaped the notice of bryologists almost completely and were overlooked even by Grout (1939) in the latest monograph of the American species of *Desmatodon*. A careful study of the present collections has led to the conclusion that much of the material from the southwestern United States identified as *Didymodon tophaceus* really belongs to the present species. For several years it has been realized that much of the so-called *Didymodon tophaceus* of California does not agree with European or with eastern North American material, and that, moreover, it differs markedly in the structure of the leaf midrib, in its darker color, the more revolute leaf margins, and in the smaller amount of carbonate deposition. The problem has been complicated by the statement of Conard (1945) to the effect that *Didymodon tophaceus* is the only one of several very similar and commonly confused species that possesses hyaline and decurrent alar cells. Since *Desmatodon hendersoni* presents the same condition, as well as other features of resemblance, some confusion has very naturally resulted between the two species. A careful reexamination of a series of specimens from the Southwest now identified as *Didymodon tophaceus* is expected to result in a very considerable extension of the geographic range of the present species, at the moment known with certainty only from the Pacific Coast states.

DIDYMODON TOPHACEUS (Brid.) Jur. Kingman's collection of this species, "Near a calcareous spring," was reported by himself (1912) and by Millspaugh and Nuttall. Several collections made in 1953 were so identified in the field, but on careful study later they all turned out to be *Desmatodon hendersoni* as indicated in the discussion of that species. An investigation of the whole problem is now under way.

*EUCLADIUM VERTICILLATUM (Brid.) BSG. Locally abundant on rock and thin soil over rocks in cascades of a small stream, in a deep shaded canyon. Common in wet calcareous habitats in California.

*PHASCUM HYALINOTRICHUM Card. & Thér. A few plants with sporophytes of this distinctive and interesting moss which is nearly microscopic in size were collected with specimens of *Fossombronia hispidissima* quite by accident as they had been confused in the field with *Bryum argenteum*. This appears to be only the third known collection of a species restricted so far to southern California. Of course, the minute size prevents its discovery, but careful search specifically for this moss during its growing season would undoubtedly result in the finding of many populations over a much wider area.

*POTTIA ARIZONICA Wareham. Very abundant in pastured valley bottom behind White's Landing; not in good condition as the capsules had

dried up before full maturation and were still mostly operculate.

*POTTIA BRYOIDES (Dicks.) Mitt. A few scattered plants of this distinctive species were found on bare soil on top of the rocky headland at White's Landing; with sporophytes.

TIMMIELLA VANCOUVERIENSIS Broth. Not uncommon on steep, shaded slopes and on the pastured valley bottom in full sun; sterile. Previously reported by Sayre (1940) as *T. anomala*, a species that may not occur in California (cf. Koch, 1950).

*TORTULA BOLANDERI (Lesq.) Broth. Abundant on moist shaded vertical soil banks near the stream in a deep canyon, at middle altitudes; with sporophytes. These specimens and a collection from San Diego (*Steere 17503*, March 24, 1952) extend the known range of the species considerably southward, from Monterey County.

*TORTULA BREVIPES (Lesq.) Broth. Common and abundant on rocky headland at White's Landing and in pastured valley bottom; with sporophytes.

*TORTULA CALIFORNICA Bartram. This collection represents the first rediscovery of a handsome and well-marked species since the collection of the type specimen in Riverside County (Bartram, 1945). It grew in small quantity on a moist vertical silt bank above the stream, in a deep canyon; with sporophytes.

TORTULA INTERMEDIA (Brid.) Brid. Rather abundant on shaded rock faces in deep canyon; with sporophytes. Reported by Millspaugh and Nuttall, as *T. montana*.

*TORTULA LAEVIPILA (Brid.) Schwaegr. On inclined tree-trunk, about six feet from the ground, in rather open forest, at middle altitudes; sterile.

TRICHOSTOMOPSIS BREVIFOLIA Bartram. On exposed soil, rocky headland at White's Landing; with few sporophytes. Koch (1950) reported this species from Santa Catalina Island from a Millspaugh collection (*4730* in part). In the Millspaugh and Nuttall list this specimen, collected at Avalon Run, is included under *Barbula artocarpa*, a badly misunderstood species.

*TRICHOSTOMOPSIS FAYAE Grout. Abundant on exposed silt in open pastured valley bottom behind White's Landing, and conspicuous for its perfectly black color, in contrast to the various shades of brown of the associated mosses.

*WEISSIA VIRIDULA Hedw. Not at all common; one colony of this customarily weedy species was found on soil at the shaded face of a large boulder, associated with *Asterella californica*; sterile.

GRIMMIACEAE

*GRIMMIA PULVINATA (Hedw.) Smith. On vertical rock, headland at White's Landing; a sterile, reduced form.

GRIMMIA TRICHOPHYLLA Grev. Not uncommon and locally abundant in several places on shaded rock-faces in deep canyons; with sporophytes. Reported from this area by Millspaugh and Nuttall; also by Sayre (1940).

FUNARIACEAE

FUNARIA HYGROMETRICA Hedw. Abundant in pastured valley bottom; with sporophytes. A truly weedy species all over the world. Reported by Millspaugh and Nuttall.

FUNARIA MUHLENBERGII Turn. On moist steep silt banks above stream in deep canyon; locally abundant, with sporophytes in several stages of development. Previously reported by Millspaugh and Nuttall.

BRYACEAE

BRYUM ARGENTEUM Hedw. var. LANATUM (Brid.) BSG. Not common, on rocky headland, White's Landing; with sporophytes. Although a truly cosmopolitan weed, this moss was not found in abundance. Reported by Millspaugh and Nuttall.

BRYUM BICOLOR Dicks. On exposed silt in pastured valley bottom; with sporophytes. Reported by Millspaugh and Nuttall as *B. californicum.*

*BRYUM CANARIENSE Brid. On moist soil, steep bank above small stream, in deep canyon; with sporophytes.

BRYUM CAPILLARE Hedw. A variable species, abundant in many forms, on soil and rock-faces; with sporophytes. Reported by Kingman (1912) under the name, *B. obconicum,* and by Millspaugh and Nuttall as *B. torquescens.*

BRYUM CUSPIDATUM (BSG.) Schimp. Common on soil, from shaded moist slopes of deep canyons to open insolated valley bottoms; with sporophytes. Reported by Millspaugh and Nuttall as *B. intermedium.*

BARTRAMIACEAE

*ANACOLIA MENZIESII (Turn.) Paris var. BAUERI (Hampe) Paris. In local abundance at White's Landing, on headland, and on shaded bank in deep canyon at some altitude; at the second locality with sporophytes. The moisture requirements of this species are such that fog must occur reasonably commonly in the places where it is found.

ORTHOTRICHACEAE

ORTHOTRICHUM CYLINDROCARPUM Lesq. Reported by Millspaugh and Nuttall from Bulrush Canyon, but not found in 1953.

ORTHOTRICHUM LYELLII Hook. & Tayl. Reported by Millspaugh and Nuttall but not found in 1953 in the White's Landing area.

*ORTHOTRICHUM TENELLUM Bruch. Common and occasionally abundant on the trunks and branches of trees in open forest in the upper reaches of a deep canyon; with sporophytes. The report of *O. cylindrocarpum* from Santa Catalina Island may be based on this species.

CRYPHAEACEAE

ALSIA CALIFORNICA (Hook. & Arn.) Sull. Reported by Millspaugh and Nuttall, but not seen in 1953.

Leucodontaceae

Antitrichia californica Sull. Reported by Millspaugh and Nuttall, but not found in 1953 in the White's Landing areas.

*Bestia breweriana (Lesq.) Grout. On base of tree in shade, in deep narrow canyon. This seems to be an extension of range southward from Monterey County; sterile.

*Bestia brevipes (Sull. & Lesq.) Broth. On shaded rock-face above stream, in deep canyon; sterile. This is not a common species anywhere (cf. Koch, 1950).

*Pterogonium gracile (Hedw.) BSG. On shaded rock-face in deep canyon, in considerable quantity but sterile. A common and widely distributed species in the state.

Thuidiaceae

Claopodium whippleanum (Sull.) Ren. & Card. Reported by Millspaugh and Nuttall but not found in 1953, even though it is a very common species almost throughout California.

Haplocladium microphyllum (Hedw.) Broth. Reported by Sayre (1940), as *Thuidium microphyllum*; not represented in the 1953 collections.

Amblystegiaceae

*Amblystegium compactum (C. Müll.) Grout. On moist soil below cascade of small stream in deep canyon; sterile. This collection establishes an interesting disjunction, as the species is otherwise known in California from the northern part.

Brachytheciaceae

Camptothecium aeneum (Mitt.) Jaeg. & Sauerb. var. dolosum (Ren. & Card.) Grout. On shaded rock-face near stream, deep canyon; with sporophytes. Reported by Millspaugh and Nuttall as *C. dolosum*.

*Camptothecium alsioides Kindb. On soil at base of tree in deep shaded canyon; with sporophytes. This is a considerable extension southward of the geographical range of a species described from Marin County and otherwise still known only from northern California.

*Camptothecium pinnatifidum (Sull. & Lesq.) Jaeg. & Sauerb. On moist shaded soil in deep canyon; sterile. This is a common and widely distributed species in California, usually on rock.

Camptothecium arenarium (Lesq.) Jaeg. & Sauerb. Reported by Millspaugh and Nuttall, but not found in 1953.

Eurhynchium pulchellum (Hedw.) Jenn. and R. pulchellum var. scabrisetum Grout. These were reported by Sayre (1940) from collections made by Cockerell. In view of the generally northern and montane distribution of the species and the eastern range of the variety, it is possible that these reports are based on *Scleropodium illecebrum*, a remarkably variable species that produces forms parallel to those of *E. pulchellum*. Attempts to obtain material of these collections for further study have been unsuccessful.

*HOMALOTHECIUM NUTTALLII (Wils.) Grout. Abundant on the base of a tree in open forest in the upper reaches of a large canyon; with sporophytes. A very common Pacific Coast species.

*SCLEROPODIUM CAESPITOSUM (Wils.) BSG. On shaded soil in deep canyon; sterile. A common Californian species.

SCLEROPODIUM CALIFORNICUM (Lesq.) Ren. & Card. On soil over rock in deep canyon; sterile. Reported from the same area by Millspaugh and Nuttall.

*SCLEROPODIUM COLPOPHYLLUM (Sull.) Grout. On soil, steep bank above stream, deep canyon; sterile. A variable species that may represent only an extreme form of one of the others listed here.

SCLEROPODIUM ILLECEBRUM (Schwaegr.) BSG. Very abundant on shaded vertical rock-faces in deep canyon; with sporophytes. This material is of more than casual interest because it differs from all other forms of the species known to the author through the presence of numerous spines on the back of the costa, at and near its apex, arranged in a pectinate fashion. However, it is hardly necessary to give nomenclatural recognition to this race, in view of the fundamental variability of the basic species. Reported by Millspaugh and Nuttall as "One of the commoner mosses of the island"; also listed by Sayre (1940).

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JOSEPH PRINCE TRACY

1879–1953

It is with a deep sense of loss that the attention of the botanical public is called to the death of Joseph P. Tracy which occurred, after a long illness, in Eureka, California, on November 26, 1953.

To the efforts of no other individual are we so beholden as we are to his for the knowledge of the flora of the northwestern counties, particularly Humboldt, which is now at our command. Although he left no legacy of publications on that flora, his large collection of specimens, which comprised a private herbarium kept at his home in Eureka and which he bequeathed to the Herbarium of the University of California, bears eloquent testimony to his devotion to his chosen field. The botanical library which he likewise left to the University indicates the thoroughness and scholarliness of his approach to the problems of the evaluation of taxa and the identification of specimens, always with due regard for the views of monographers. He corresponded with botanical specialists and, when his own efforts did not satisfy him, he submitted many of his critical specimens to them for their expert opinions. Mr. Tracy's field work extended over the last fifty years of his life, during which period he presented to both the Jepson and the University herbaria, but mostly to the latter, some thirty thousand of his duplicates. Many of these were distributed to herbaria throughout the world where they now reside as valued accessions. More than a few of his specimens have formed the basis for new species, many of which have been named for him. In 1937, Dr. S. F. Blake published in his honor the genus *Tracyina* as an entirely new entity (*T. rostrata*) in the Compositae.

Mr. Tracy was born on January 11, 1879, in Hydesville, Humboldt County, California, in the low broad valley formed where the Eel and Van Duzen rivers meet. His parents, both of New England stock, were Joseph Tracy and Harriet Morris, and from his father, who surveyed many of the roads and land lines in the early northern California of that day, young Joe acquired his interest in the land which was later to lead

to his choice of vocation. Despite his outdoor activities, he was not a strong boy, uninclined in consequence to compete in the more rigorous activities of boys of his own age. Instead he was wont to wander in the nearby redwoods and grassy hillsides, storing up the impressions which were to culminate in his avocational devotion to matters botanical. His mother's family settled on a ranch on Howell Mountain near St. Helena in Napa County, which later was acquired by the University of California and is now known as "Las Posadas State Forest." There Joe spent summer vacations visiting his uncle, John M. Morris, who owned the ranch, whence many of the "extra-territorial" specimens of earlier days in Tracy's collections.

When Joe was eleven years old, his family moved to Eureka, which subsequently became his permanent home. His father was Register of Public Lands there, and Joe spent much time working with him, gaining an intimate knowledge of land titles and an appreciation of their importance. Meanwhile, he attended high school in Eureka, graduated with the first class and was among the first students who entered the University of California from Eureka. At the University, his interest in science soon became dominant, and he devoted much of his work there to botany, chemistry and physics. Among his instructors in botany were the young H. M. Hall and Dr. J. Burtt Davy, while his heightening interest in his now chosen field was directed by both Dr. Jepson and Dr. Setchell. During this time he served as a student assistant in the Herbarium. Notable among his classmates were Herbert M. Evans and E. B. Babcock.

During Mr. Tracy's final college year his father died, necessitating his return to Eureka to take upon himself the support of his mother and a younger brother and sister, but he returned to finish his college work. Despite the handicaps, he was honored with memberships in both Phi Beta Kappa and Sigma Xi and succeeded in earning his A.B. in three and a half years, thus graduating with the class of 1903. He had hoped to return later for graduate work and higher degrees, intentions which he never was able to realize. Nevertheless, through the years, he maintained, to mutual advantage, a close association with colleagues at the University of California and the California Academy of Sciences.

Upon his return to Eureka in 1904, he looked for suitable employment. His early training in land surveying with his father came to his aid in this connection, and he soon found congenial employment with the Belcher Abstract and Title Company, by which firm he was employed until his death. "By those who had occasion to require . . . . service in the matter of the authentication or clearance of land titles", Joseph Tracy "was acknowledged as an expert in this field, and deeds, titles and other documents relating to land ownership or transfer . . . . bear the imprint of his training, skill and judgment," as the "Humboldt-Standard" editorialized in its obituary notice.

All the while, he followed his botanical bent as an avocation, collecting in his spare time. He was a familiar sight in the woods and hills of the

northwestern counties, with his plant press and his fish-creel, and during deer season, his gun, in his ofttimes well-worn Ford car on the less frequented byways of his district. His fine collection of horns on the walls of his home herbarium bore witness to his marksmanship, for almost every year, Joe "brot home his buck." Besides his abiding concern with the plant life of the region, Joe's kindred interests extended to an acquaintance as well with the soils and geological formations he encountered.

Another interest was music, and for many years his true tenor voice was heard in his church choir and in the choral societies of which he was so devoted a member.

Mr. Tracy was generous of his time and interests, happy to aid any one who showed a genuine interest in natural history. He was glad to help students and spent many an evening with them, feeling amply rewarded by their later accomplishments in the botanical field. He cooperated often with County Farm Advisors, while never a summer passed without several visits from fellow botanists and students.

In his later years, his plant collections extended more and more to counties other than Humboldt and adjacent Trinity County. On his forays into Del Norte and contiguous Siskiyou County and southwestern Oregon, he made many joint collections, a large share of them mycological, with Mr. Harold Parks of Trinidad, formerly of the Department of Botany at the University of California. His frequent collecting trips to Trinity Summit and the Salmon Mountains were facilitated by his possession of a cabin and a plot of land close to that of one of his sisters at Willow Creek. Frequently accompanying him on these trips were his brother-in-law, Judge Frank A. Graham of Willow Creek, and his young nephew, Joseph T. Gregory, who later joined the staff of the Peabody Museum of Paleontology at Yale University.

Mr. Tracy is survived by two sisters, Mrs. Harriett Graham of Willow Creek, and Miss Ethel Tracy of Eureka, who so kindly supplied many of the biographical details, especially of Joe's earlier life, as well as by two nieces, Mrs. Phillip DeLong of Eureka and Miss Grace Tracy of Oakland, and by his nephew, Dr. Joseph T. Gregory of New Haven, Conn.

In addition to his membership in the California Botanical Society, Mr. Tracy took an active part in the work of the Save-the-Redwoods League and was a member of the following societies: American Association for the Advancement of Science, American Geographic Society and the California Academy of Sciences.

Joe Tracy is recalled by his friends and all who knew him as a gentle, kindly, and modest gentleman, generous of himself and eager to share his knowledge. He was highly respected and valued by his business associates and by those who sought his expert assistance on title and documentary matters. His lasting monument is embodied in the large and significant personal herbarium which is soon to be incorporated into that of the University of California.—RIMO BACIGALUPI, Department of Botany, University of California.